

# Behavioral Thermoregulation in *Hemigrapsus nudus*, the Amphibious Purple Shore Crab

I. J. McGAW

*Department of Biological Sciences, University of Nevada Las Vegas, 4505 Maryland Parkway,  
Las Vegas, Nevada 89154-4004; and Banfield Marine Sciences Centre, 100 Pachena Road,  
Banfield, British Columbia V0R 1B0, Canada*

**Abstract.** The thermoregulatory behavior of *Hemigrapsus nudus*, the amphibious purple shore crab, was examined in both aquatic and aerial environments. Crabs warmed and cooled more rapidly in water than in air. Acclimation in water of 16 °C (summer temperatures) raised the critical thermal maximum temperature (CTMax); acclimation in water of 10 °C (winter temperatures) lowered the critical thermal minimum temperature (CTMin). The changes occurred in both water and air. However, these survival regimes did not reflect the thermal preferences of the animals. In water, the thermal preference of crabs acclimated to 16 °C was 14.6 °C, and they avoided water warmer than 25.5 °C. These values were significantly lower than those of the crabs acclimated to 10 °C; these animals demonstrated temperature preferences for water that was 17 °C, and they avoided water that was warmer than 26.9 °C. This temperature preference was also exhibited in air, where 10 °C acclimated crabs exited from under rocks at a temperature that was 3.2 °C higher than that at which the 16 °C acclimated animals responded. This behavioral pattern was possibly due to a decreased thermal tolerance of 16 °C acclimated crabs, related with the molting process. *H. nudus* was better able to survive prolonged exposure to cold temperatures than to warm temperatures, and there was a trend towards lower exit temperatures with the lower acclimation (10 °C) temperature. Using a complex series of behaviors, the crabs were able to precisely control body temperature independent of the medium, by shuttling between air and water. The time spent in either air or water was influenced more strongly by the temperature than by the medium. In the field, this species may experience ranges in temperatures

of up to 20 °C; however, it is able to utilize thermal microhabitats underneath rocks to maintain its body temperature within fairly narrow limits.

## Introduction

Intertidal organisms experience abrupt, frequently large, changes in temperature as a result of alternating episodes of exposure to air and water (Vernberg and Vernberg, 1972). These changes in temperature may pose an additional burden to amphibious organisms that are already challenged by the switch between ventilatory media (Greenaway *et al.*, 1996).

*Hemigrapsus nudus*, the purple shore crab, is a common species in the mid- to high-intertidal zone of rocky shores along the northeastern Pacific (Schmitt, 1921; Dehnel, 1960; Low, 1970; Daly, 1981). These crabs are involuntarily exposed as the tide recedes, but they are active in air (Burnett and McMahon, 1987). The species can tolerate temperatures up to 33.6 °C for short periods of time (Todd and Dehnel, 1960); however, exposure to suboptimal temperature regimes is associated with compensatory physiological responses in decapod crustaceans.

The aerobic metabolism of crustaceans, like that of most other aquatic organisms, is temperature dependent. Oxygen uptake increases in *Carcinus maenas*, the green shore crab, as the temperature of the water is raised (Taylor and Wheatly, 1979); likewise, oxygen consumption in *Homarus gammarus*, the European lobster, decreases (for a short time) as temperature is lowered (Whiteley *et al.*, 1995). Increases in temperature also influence oxygen delivery to the tissues by causing a reduction in the carrying capacity of the hemolymph for oxygen and the binding of oxygen to the hemocyanin (Taylor, 1981; Truchot, 1983).

Heart rate is directly related to temperature in a number

of crustacean species (deFur and Mangum, 1979; Taylor and Wheatly, 1979; DeWachter and McMahon, 1996; Stillman and Somero, 1996; Pirro *et al.*, 1999; Jury and Watson, 2000; Fredrich *et al.*, 2000). Heating increases heart rate and cardiac output but decreases stroke volume in *Cancer magister*, the Dungeness crab (DeWachter and McMahon, 1996). This is associated with an increase in hemolymph perfusion of the carapace, gonads, and musculature of the pereopods (DeWachter and McMahon, 1996). Cooling causes a decrease in cardiac parameters: heart rate and cardiac output drop sharply in low temperature, and hemolymph flow is directed away from anterior structures to more ventral structures (Fredrich *et al.*, 2000).

Since exposure to high or low temperatures can be metabolically costly, the ability of crabs to sense temperature and orient to a "thermal niche" should be advantageous in minimizing physiological stress. In addition, many processes such as molting, growth, reproduction, and maturation of eggs are temperature dependent (Sastry, 1983a, b); therefore, selection of optimal temperatures should also maximize growth and reproductive potential (Hutchison and Maness, 1979). A number of crustacean species are known to exhibit behavioral thermoregulation. *Homarus americanus*, the American lobster, can thermoregulate precisely for up to 6 days, preferring temperatures in the 15–21 °C range (Reynolds and Casterlin, 1979a; Crossin *et al.*, 1998). Lobsters are able to detect water temperature differences of as little as 1 °C and exhibit directional taxis (Jury and Watson, 2000). *Carcinus maenas*, the green shore crab, avoids adverse temperatures, showing emersion responses at 28 °C in the laboratory (Taylor and Wheatly, 1979). *Procambarus clarkii*, the red swamp crayfish, has a broad temperature tolerance (Payette and McGaw, 2001) and prefers water with a mean temperature of 23–24 °C (Espina *et al.*, 1993; Ramirez *et al.*, 1994). An animal's thermal preference can be also be influenced by the acclimation temperature. Acclimation to warm temperatures results in a higher temperature preference in *Homarus americanus*, the American lobster (Crossin *et al.*, 1998), and in *Astacus astacus*, a crayfish (Kivivuori, 1994). Temperature acclimation has an opposite effect on the crayfish *Orconectes immunis*, with animals acclimated to warm water selecting cooler temperatures than those acclimated to cold water (Crawshaw, 1974).

Most of the articles on behavioral thermoregulation in decapod crustaceans have concentrated on fully aquatic species (see Crossin *et al.*, 1998). Much less information exists on amphibious species that are emersed in the intertidal zone twice daily (Thurman, 1998). *H. nudus* is exposed to a wide range of temperatures on both a tidal and diurnal basis (Todd and Dehnel, 1960; Greenaway *et al.*, 1996). Therefore, the aim of this study was to investigate the thermal ecology of this amphibious species and to assess the

role of behavioral reactions, in both water and air, in minimizing the effects of thermal stress.

## Materials and Methods

Adult male and female purple shore crabs, *Hemigrapsus nudus*, of 25–40-mm carapace width, were collected intertidally in Barkley Sound, British Columbia, during the months of May to August in 2000 and 2001. They were transferred to 40-liter aquaria at the Bamfield Marine Sciences Centre and maintained in aerated seawater at a salinity of 33 ppt  $\pm$  0.5 ppt on a natural light-dark cycle. The crabs were held at water temperatures of either 16 °C  $\pm$  0.5 °C or 10 °C  $\pm$  0.5 °C for at least 2 weeks. These temperatures approximated those measured in the field during summer and winter respectively (Gosselin and Chia, 1995). More extreme temperatures were not used because the animals tended to molt at higher temperatures and become lethargic at lower temperatures. The crabs were fed sea lettuce, *Ulva lactuca*, *ad libitum*. Approximately equal numbers of each sex were used, and individual crabs were not re-used in any experiment.

### Rate of change of body temperature

Changes in the body temperature of *H. nudus* ( $n = 10$ ) were studied in water and air. To measure blood temperature, a catheter-mounted (PE90) thermocouple (Physitemp IT18) was inserted through a small hole drilled in the first abdominal segment and guided to lie against the sternal artery. The crabs were returned to the holding tank and allowed to settle for 15 min. Animals ( $n = 10$ ) were then transferred to water or air of 5 °C or 20 °C. The amount of time required for the body temperature to equilibrate with the surrounding medium was recorded at 30-s intervals using a BAT 12 digital thermometer (Physitemp Instruments).

### Critical thermal maximum and minimum temperatures

The critical thermal maximum (CTMax) and critical thermal minimum (CTMin) temperatures of *H. nudus* were assessed in air and in water ( $n = 30$ ). Crabs were acclimated to 10 °C or 16 °C and were studied separately, with the starting temperature being 10° or 16 °C, respectively. The temperature of the air was raised (or cooled) at 0.5 °C/min in an incubator (Percival Instruments [Boone, Iowa]; model 135LL), and the temperature was monitored at 1-min intervals with a Physitemp BAT12 digital thermometer. A volume of 5 liters of water was used, and the temperature was raised (or cooled) at 0.5 °C/min by way of a recirculating water bath (VWR Scientific Instruments). The water was aerated, and the temperature was monitored with the Physitemp thermometer. At random intervals, the crabs were turned on their backs until the first animal

reached its CTMax or CTMin; that is, until the animal could no longer right itself within 1 min (Cuculescu *et al.*, 1998). Thereafter, all remaining crabs were inverted together every minute and the CTMax or CTMin was recorded for each individual.

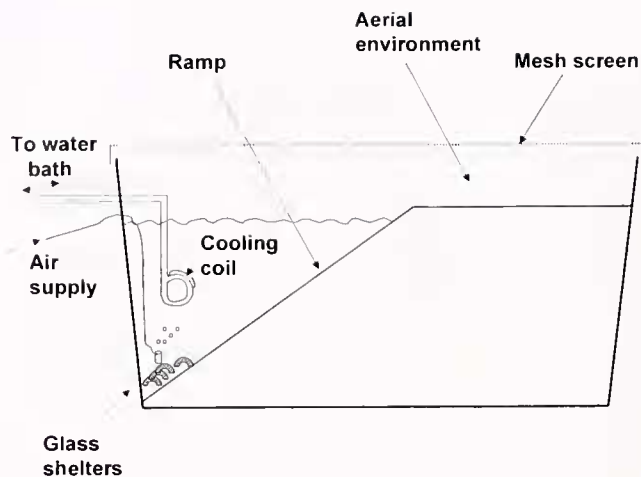
#### Temperature preference behavior

The temperature preference range of *H. nudus* was determined using an elongated (length, 300 cm) cylindrical (diameter, 12 cm) chamber that was orientated horizontally. Heating and cooling recirculating water baths at either end of the chamber maintained the temperature gradient between 7 °C and 30 °C. The placement of the heating and cooling water baths was alternated between each trial, to eliminate any bias for either end of the chamber. Airstones minimized any vertical thermal stratification in the gradient and ensured that the water did not become hypoxic. Shelters (broken glass beakers) were placed along the length of the chamber to reduce stress, *H. nudus* is highly thigmotactic and will remain active, attempting to escape, unless there is a place to shelter (McGaw, 2001). This atypical behavior could obscure thermoregulatory responses. Crabs—a maximum of five at any one time (8 repetitions; total  $n = 40$ )—were introduced into the gradient at random locations; using this number of *H. nudus* in experiments does not affect the thermotolerance of an individual (Todd and Dehnel, 1960). After 3 h, a temperature reading was taken at the position of each individual crab. Those crabs acclimated to either 10 °C or 16 °C were studied separately. In control experiments, the temperature was maintained at either a constant 10 °C or a constant 16 °C; crabs were then introduced randomly into the apparatus, and their position was recorded after 3 h.

#### Temperature avoidance

The following two experiments were designed to test the responses of the crabs after they had sensed a change in temperature. Behavioral responses consisted of migration from underneath a shelter as the temperature changed. Experiments were performed in both aquatic and aerial environments.

The first experiment (aquatic) was carried out in a modified two-choice chamber (Fig. 1), which contained seawater (32 ppt), in one side, as well as pieces of broken glass beakers for shelter. The chamber was held in an incubator (Percival Instruments Model 135LL), which allowed independent control of air temperature. Five animals per trial (5 repetitions;  $n = 25$ ) were placed in the seawater and allowed to settle for 30 min. Any animals that exited the water within this period were not used in the experiments. The starting temperature of experiments was either 10 °C or 16 °C for each group of acclimated crabs. The temperature of the seawater was raised at 0.5 °C/min using a recirculat-



**Figure 1.** Modified two-choice chamber used to measure exit temperatures from water into air, shuttling behavior between air and water, and behavioral control of body temperature.

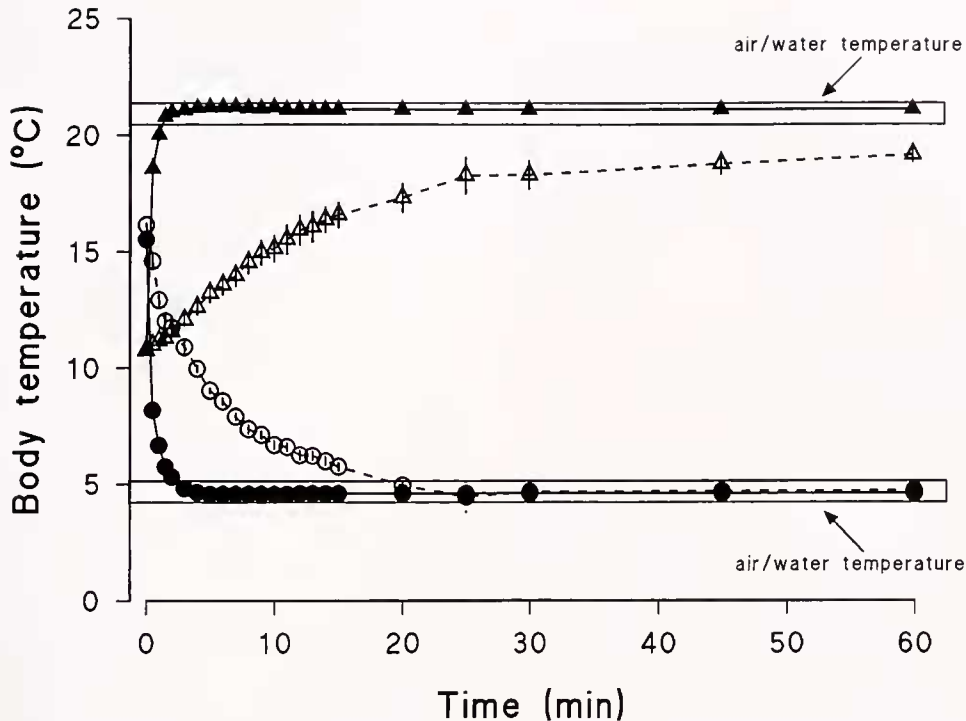
ing water bath (VWR Scientific Instruments). The temperature at which the crabs made a voluntary migration into air was recorded; this behavior was defined as "emigration" (Taylor and Wheatly, 1979). The experiment was repeated with air temperatures of 5 °C, 20 °C, and 35 °C, each at 50%–70% relative humidity. Experiments were then carried out to assess the lower preference range. The water was cooled at 0.5 °C/min, and emigration temperature from the seawater was recorded at the three air temperatures. The water side of the chamber was alternated between trials to avoid any preference associated with either side of the chamber.

For the second experiment, temperature avoidance was tested in air using a chamber measuring 45 cm × 45 cm × 8 cm deep, with a gauze bottom to allow air to circulate. Flat tiles were placed in the chamber. Five animals were then introduced into the chamber and allowed to settle under the tiles. Any animals that migrated from under the tiles within 30 min were not used in the experiments. The chamber was held in an incubator (Percival Instruments), with the starting temperature for the two acclimated groups being either 10 °C or 16 °C. The air temperature was then raised by 0.5 °C/min, and the temperature (measured under the tiles) at which the crabs exited from under the tile shelters was recorded ( $n = 25$ ). The experiment was repeated by lowering the temperature, by 0.5 °C/min, and observing the temperature at which the crabs exited from under the shelters. All recordings were made in constant dim red light.

#### Shuttling behavior

A time-lapse video recorder and camera (Panasonic AG-RT600AS VCR and Panasonic WV-BP120 camera) was used to monitor the shuttling behavior of individual crabs





**Figure 2.** Changes in body temperature (mean  $\pm$  SEM) of 10 *Hemigrapsus nudus*, after transfer from 10 °C water to 20 °C air ( $\Delta$ ), from 10 °C water to 20 °C water ( $\blacktriangle$ ), from 16 °C water to 5 °C air ( $\circ$ ), and from 16 °C water to 5 °C water ( $\bullet$ ). In some cases error bars are smaller than the symbols.

between air and water at temperatures of 10 °C, 20 °C, and 30 °C. The choice chamber was set up in an incubator with glass shelters in both air and water. Four crabs (acclimated to 16 °C) were placed in the water (2 repetitions, total  $n = 8$  for each treatment). The number of shuttles, duration of shuttles, and total time spent in air and water were recorded over a 24-h period in constant dim red light.

#### *Behavioral control of body temperature*

The body temperature of eight crabs (acclimated to 16 °C) was recorded with a thermocouple (Physitemp IT 18) introduced through the first abdominal segment. The thermocouple was connected to a BAT 12 digital thermometer (Physitemp Instruments); data were recorded on an ADInstruments Powerlab data acquisition package. The two-choice chamber was placed in an incubator (Percival, model 135LL), and a recirculating water bath allowed independent heating or cooling of the seawater. An animal was initially placed in the shallow water, and the change in its body temperature was followed for 12 h as it shuttled between air and water. A variety of water and air temperature combinations were offered, separated by differing increments.

#### *Regulation of body temperature in the field*

Regulation of body temperature was assessed in freshly collected crabs in the field. Crabs were fitted with thermo-

couples (Physitemp IT18) on a 2-m lead ( $n = 5$ ). Each crab was released on a falling high tide and allowed to settle; body temperature was recorded at half-hour intervals until the following high tide, using a BAT12 digital thermometer (Physitemp Instruments). At the same time, air temperatures were recorded 5 cm above the rock surface, and seawater temperature was recorded at the low tide, using a Physitemp IT14 thermocouple calibrated against a mercury thermometer. Experiments were repeated on days when air temperatures were higher or lower than the ambient seawater temperature.

## **Results**

#### *Rate of change of body temperature*

An increase or decrease in water temperature of about 10 °C resulted in a rapid change in body temperature (Fig. 2). Body temperature equilibrated with the surrounding water, within 2–3 min. In air, body temperature changed more slowly, and heat loss from the body was more rapid than heat gain. The body temperature took 25 min to equilibrate to a 10 °C drop in air temperature, but it failed to reach equilibrium with the surrounding air within the 60-min experimental period when the temperature was raised by 10 °C. Although body temperature reached 90% of the final temperature within 20 min, it increased slowly thereafter.

Table 1

*Thermal preference of Hemigrapsus nudus with increasing temperature*

Air temperature (°C)	Water temperature (°C) at emigration*	
	Crabs acclimated to 10 °C	Crabs acclimated to 16 °C
5	25.5 ± 0.81	25.3 ± 0.68
20	27.4 ± 0.61	24.7 ± 0.39
35	27.9 ± 0.66	25.7 ± 0.53

\* Mean (± standard error of the mean) upper temperature at which crabs ( $n = 25$ ) emigrated from water into air with a temperature of 5 °C, 20 °C, or 35 °C as the temperature of the water was raised.

### Critical thermal maximum and minimum temperatures

In water, the CTMax of 31.1 °C ± a standard error of the mean (SEM) of 0.16 °C for crabs acclimated to 10 °C was significantly lower than the CTMax of 33.6 ± 0.11 °C for crabs acclimated to 16 °C (Student's  $t$  test = -2.32,  $P = 0.02$ ). The difference between the two acclimation groups was greater in air. Crabs acclimated to 10 °C had a CTMax of 33.2 ± 0.34 °C, which was significantly lower than the CTMax of 35.3 ± 0.5 °C for 16 °C acclimated animals ( $t$  test = -3.45,  $P = 0.001$ ). In addition, the CTMax values in water were significantly lower than those in air (ANOVA,  $F = 7.55$ ,  $P = 0.007$ ).

Acclimation to either 10 °C or 16 °C also affected the critical thermal minimum temperature. The CTMin in water of 3.5 ± 0.14 °C for crabs acclimated to 10 °C was significantly lower than the 4.82 ± 0.14 °C for 16 °C acclimated crabs ( $t$  test = -6.71,  $P < 0.001$ ). A similar trend was observed in air, with CTMin values of 3.44 ± 0.15 °C and 3.99 ± 0.12 °C, for 10 °C and 16 °C acclimated crabs, respectively ( $t$  test = -2.89,  $P = 0.005$ ). As with CTMax, there was a significant effect associated with the medium: the CTMin values in air were significantly lower than those in water (ANOVA,  $F = 10.41$ ,  $P = 0.002$ ).

### Temperature preference

When 40 crabs (again, acclimated to either 10 °C or 16 °C) were placed randomly in a thermal gradient of 7 °C to 30 °C, there was considerable movement within the first 30 min. Temperature selection appeared to be complete after 3 h, with very little movement in the gradient thereafter. Although a small percentage of the crabs selected the extreme temperatures of 7 °C or 30 °C, most were distributed between 11 °C and 24 °C. The mean preference range of 17.01 °C ± 0.65 °C SEM for 10 °C acclimated crabs was significantly higher than the 14.60 °C ± 0.78 °C selected by 16 °C acclimated crabs ( $t$  test = 2.37,  $P = 0.02$ ). Control experiments were carried out for the two acclimation tem-

peratures, with no thermal gradient. Control crabs did not show a preference for any area of the gradient tank.

A similar effect of acclimation on temperature preference was observed in the temperature-avoidance experiments. When the temperature of the water was gradually increased, crabs exited from under the shelters and started to become active between 19–21 °C, but did not leave the water at this temperature. Although there were three different air temperatures that crabs could emigrate into, the air temperature had no significant effect on emigration temperatures from water (Table 1) (ANOVA,  $F = 2.47$ ,  $P = 0.088$ ). Since air temperature had no effect on behavior, data for the three air temperatures was pooled. There was a significant behavioral effect based on acclimation: crabs acclimated to 10 °C had a mean emigration temperature of 26.94 ± 0.24 °C; this was significantly higher than the mean emigration temperature of 25.25 ± 0.19 °C for crabs acclimated to 16 °C (ANOVA,  $F = 10.47$ ,  $P = 0.002$ ). All crabs had left the water when the temperature reached 34 °C.

Although all crabs left the water when the temperature was raised, this was not the case when the water temperature was lowered. Only 45% of the crabs acclimated to 10 °C and 30% of the crabs acclimated to 16 °C emigrated from the water. The rest of the crabs remained in the water even though the temperature was reduced below their CTMin, incapacitating them. Statistical results for the animals that exhibited emigration behavior are given in Table 2. Air temperature had no significant effect on the emigration temperature of the crabs (ANOVA,  $F = 0.14$ ,  $P = 0.87$ ). Although the mean emigration temperature of 4.95 ± 0.31 °C for 10 °C acclimated animals was lower than the 5.79 ± 0.42 °C for 16 °C acclimated crabs, this difference was statistically insignificant (ANOVA,  $F = 2.58$ ,  $P = 0.113$ ).

Therefore, in water, 10 °C acclimated crabs have a preference range between 4.95 °C and 26.94 °C, with a mean preference of 17.1 °C. The crabs acclimated to 16 °C have a mean temperature preference of 14.60 °C with a narrower preference range between 5.79 °C and 25.25 °C.

Acclimation to either 10 °C or 16 °C had a similar effect on temperature avoidance in air. When the temperature of

Table 2

*Thermal preference of Hemigrapsus nudus with decreasing temperature*

Air temperature (°C)	Water temperature (°C) at emigration*	
	Crabs acclimated to 10 °C	Crabs acclimated to 16 °C
5	4.72 ± 0.53	5.87 ± 0.51
20	5.23 ± 0.57	5.24 ± 0.61
35	4.91 ± 0.66	6.26 ± 0.89

\* Mean (± standard error of the mean) temperature at which crabs ( $n = 25$ ) emigrated from water into air with a temperature of 5 °C, 20 °C, or 35 °C as the temperature of the water was lowered.

Table 3

Shuttling behavior of *Hemigrapsus nudus* from water into air when both media were maintained at 10 °C, 20 °C, or 30 °C

Temperature (°C)	Parameter*		
	Number of shuttles	Duration of each shuttle (min)	Percent time spent in air/24 h
10	26.4 ± 5.1	8.6 ± 0.9	16.6 ± 11.3
20	18.0 ± 4.3	21.2 ± 8.1	24.5 ± 23.5
30	27.3 ± 6.2	28.5 ± 7.5	64.3 ± 16.5

\* Values are the mean (± standard error of the mean) response for 8 crabs.

the air was gradually raised, the crabs exited from under tiles in an attempt to escape. The mean exit temperature for crabs acclimated to 10 °C was  $27.39 \pm 0.62$  °C; this was significantly higher than the exit temperature of  $24.17 \pm 0.58$  °C recorded for 16 °C acclimated crabs ( $t$  test =  $-3.8$ ,  $P < 0.001$ ). Consistent with lower emersion temperatures in water, not all crabs exited from under shelters as the air temperature was gradually reduced. Five of the 25 crabs acclimated to 10 °C remained under the shelters, while 10 of the crabs acclimated to 16 °C did not exit. Statistical analysis includes only the animals exhibiting this exit behavior. Although the mean exit temperature of  $4.36 \pm 0.47$  °C recorded for 10 °C acclimated crabs was lower than the  $5.85 \pm 0.7$  °C recorded for 16 °C acclimated animals, this difference was statistically insignificant ( $t$  test =  $-1.82$ ,  $P = 0.077$ ). Therefore, the temperature preference range in air for 10 °C acclimated crabs was 4.36 °C to 27.39 °C, which was broader than that for 16 °C acclimated animals (5.85 °C to 24.17 °C).

### Shuttling behavior

The shuttling movement of 16 °C acclimated crabs between air and water was studied during a 24-h period to determine the number and duration of excursions into air (Table 3). There was no significant difference in the number of shuttles between air and water as a result of ambient temperature (ANOVA,  $F = 0.96$ ,  $P = 0.4$ ). There was a trend towards an increase in the average duration of each excursion into air as the temperature increased, but it was not statistically significant (ANOVA,  $F = 3.01$ ,  $P = 0.05$ ). When the percentage of time (per 24-h period) that each crab spent in air was considered, a significant pattern emerged (Table 3). As the temperature increased, the crabs spent a significantly greater total percentage of time in air (ANOVA,  $F = 14.72$ ,  $P < 0.001$ ). The percent of time that the crabs spent in air at 30 °C was significantly higher than time spent in 10 °C and 20 °C conditions, but there was no significant difference between 10 °C and 20 °C (Tukey test,  $q = 1.18$ ,  $P = 0.684$ ).

### Behavioral control of body temperature

When offered a choice of 20 °C water with 8 °C air (trial 5), the crabs remained in the water most of the time; the mean body temperature of  $20.3$  °C  $\pm 0.2$  °C SD was not significantly different from the water temperature (Fig. 3). The body temperature in experimental trial 5 was significantly higher than in the other trials (Tukey test,  $P < 0.05$ ). In experimental trial 4 (14 °C water and 24 °C air), the crabs also remained in the water; again, the mean body temperature of  $14.2 \pm 0.3$  °C was not significantly different from that of the water (Fig. 3). In all other trials, the crabs maintained the body temperature at levels between the temperature of the air and the water. In the shallow water of the chamber, periodically, a crab either raised or submerged itself to control its body temperature between mean values of  $7.7 \pm 0.9$  °C and  $14.6 \pm 1.5$  °C.

Examination of the body temperature of individual crabs shows the thermoregulatory responses in more detail (Fig. 4a–d). When the water was held at 4–5 °C and the air at 33–34 °C (Fig. 4a), the crab spent the first 2 h shuttling

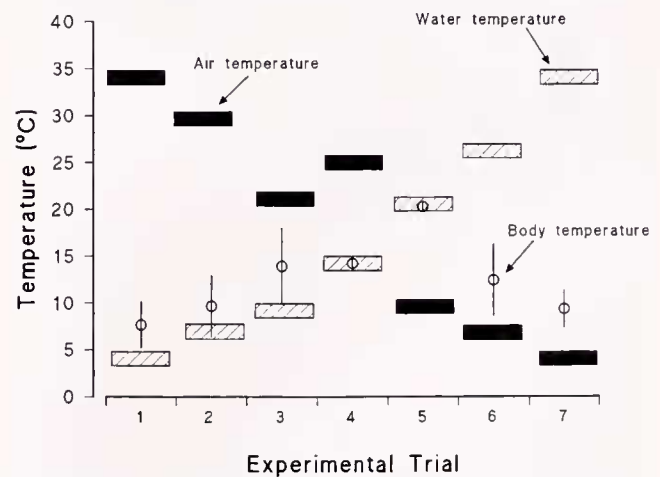
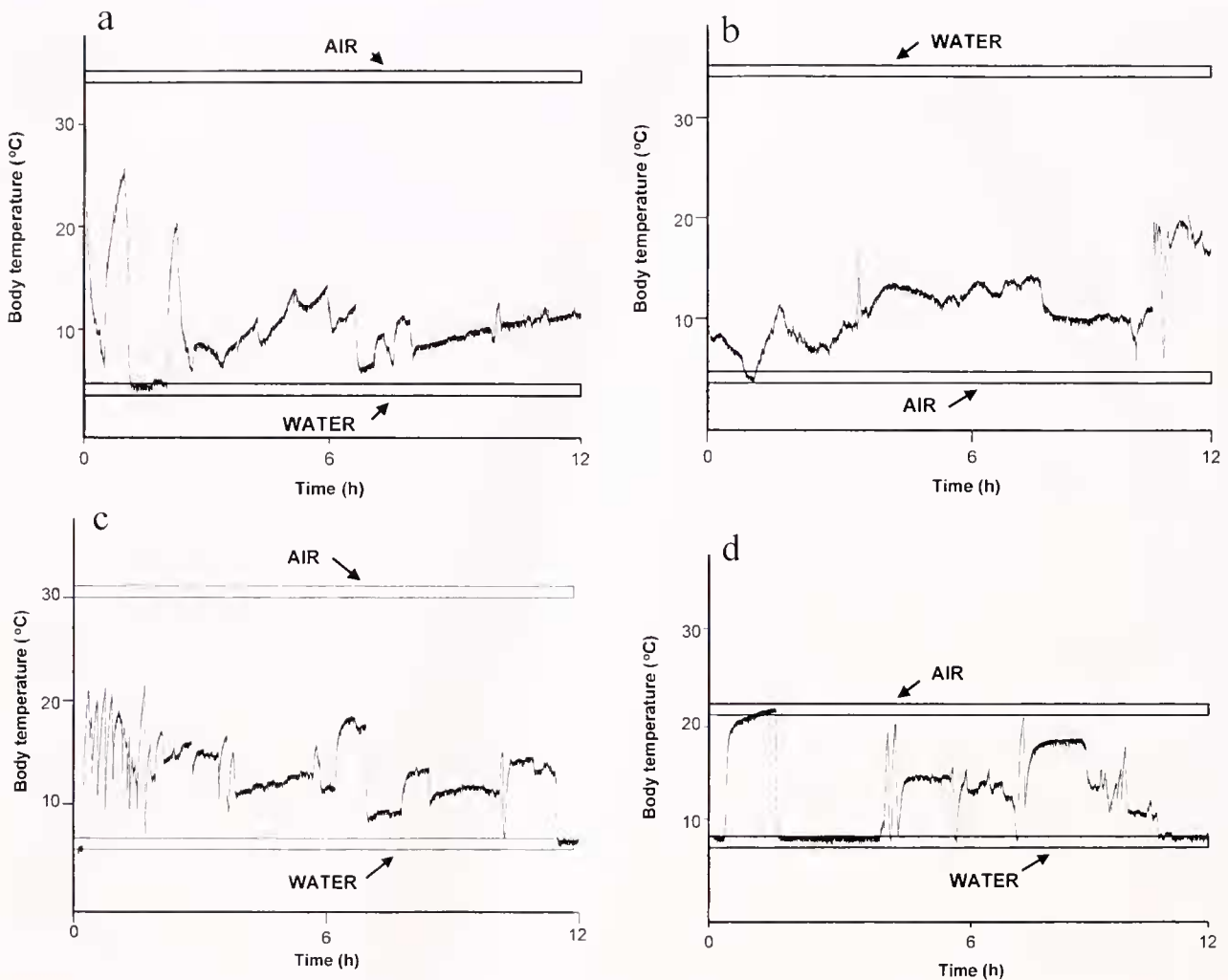


Figure 3. Mean body temperature ( $\pm$ SD) of *Hemigrapsus nudus* ( $n = 8$ ) when offered a choice between air and water, maintained at different temperatures relative to one another. Hashed bars represent water temperature, and solid bars represent air temperatures.



**Figure 4.** Representative examples of body temperatures of individual *Hemigrapsus nudus* in a two-choice chamber with the ability to shuttle between air and water of different temperatures. (a) Water of 4–5 °C and air of 33–34 °C. (b) Water of 33–34 °C and air of 4–5 °C. (c) Water of 6–7 °C and air of 30–31 °C. (d) Water of 8–9 °C and air of 20–21 °C.

between air and water, after which it raised or submerged itself in the water to maintain a body temperature of about 8–13 °C. When the temperatures of the air and water were reversed (4–5 °C air and 33–34 °C water), the crab (Fig. 4b) was still able to maintain a body temperature between 8 and 13 °C for most of the 12-h experimental period. When the difference between air and water was decreased (8–9 °C water and 29–30 °C air), body temperature fluctuated somewhat during the first 2 h when the crab was active; thereafter, body temperature was maintained between 10 °C and 17 °C (Fig. 4c). When air and water temperatures (20–21 °C air and 8–9 °C water) approached limits within the animal's preference range (Table 1, 2), the crab tended to shuttle back and forth between air and water, spending extended periods of time in either medium, where body temperature equilibrated with the medium (Fig. 4d).

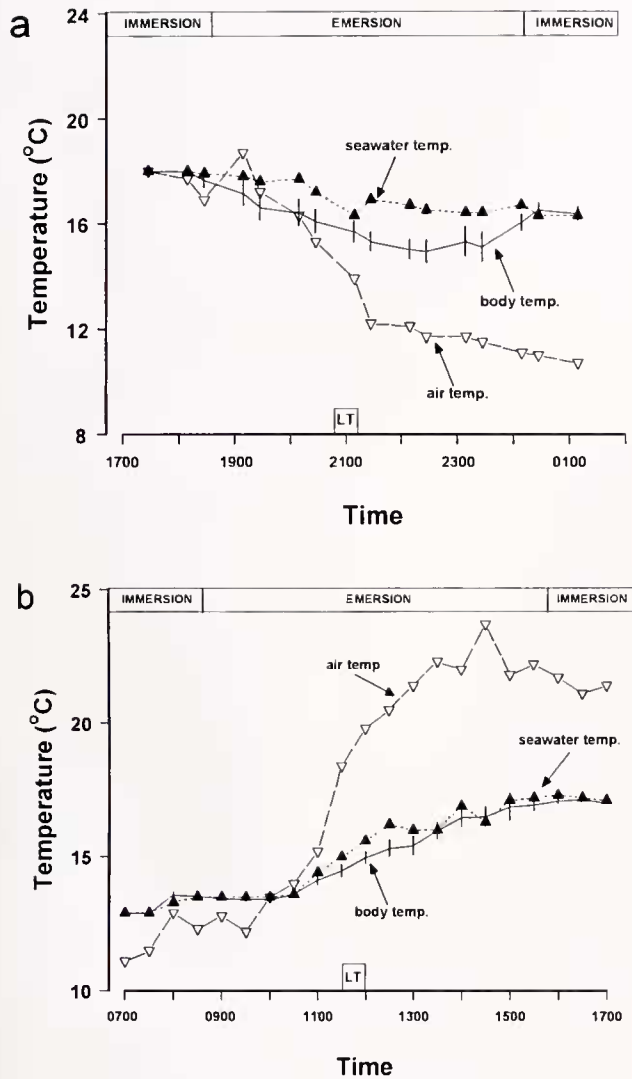
#### *Body temperature in the field*

Changes in body temperature of *H. nudus* were recorded in the field during an intertidal period (Fig. 5). Body temperature was monitored on a cold day (Fig. 5a), when the air temperature dropped below that of the seawater. Although air temperatures fell from 18 °C to 10.7 °C, body temperatures decreased only slightly. The mean body temperature of the crabs ( $n = 5$ ) dropped from  $17.65 \pm 0.28$  °C SEM when initially emerged, down to  $14.92 \pm 0.44$  °C at the end of the intertidal period. This was only a 16% drop in body temperature, compared to a drop of 41% in the temperature of the surrounding air. Body temperature increased rapidly when the crabs were re-immersed, reaching  $16.5 \pm 0.27$  °C as it equilibrated with the seawater.

On a warm day (Fig. 5b) the air temperature quickly rose



## Discussion



**Figure 5.** Changes in body temperature (mean  $\pm$  SEM) of 5 specimens of *Hemigrapsus nudus* (solid line) in the intertidal zone. Crabs were released during a falling tide and monitored until the following high tide. Seawater temperatures (dotted line, solid symbols) and air temperatures (dashed line, open symbols) were also recorded during this time. Times of emersion and immersion of the crabs, as well as low tide (LT), are indicated on the graphs. Recordings were made on (a) 8 July 2001, when surrounding air temperatures were lower than ambient seawater temperatures and (b) 23 July 2001, when air temperature was higher than seawater temperature.

from 11 °C in the morning to 22–24 °C by early afternoon. Despite this 12 °C rise in air temperature, the body temperatures of the crabs did not change as rapidly, and reached only  $16.86 \pm 0.51$  °C by the end of exposure period in air. The change in body temperature was similar to the observed increase in seawater temperature during the day (Fig. 5b). When the crabs were re-immersed, their body temperatures quickly equilibrated with the seawater.

The observed rates of change in body temperature (Fig. 2) were similar to those reported previously for *Hemigrapsus nudus* (Greenaway *et al.*, 1996). In lobsters, heat loss in air is more rapid than heat gain (Whiteley *et al.*, 1995); this was also observed here for *H. nudus* (Fig. 2), probably due to the evaporative heat loss in air. During these experiments, several of the crabs regurgitated frothed fluids from the stomach, smeared this over the ventral carapace with the chelae, and raised their body above the substrate. This foaming behavior has been reported for a number of crab species (Lindeberg, 1980; Maitland, 1990) and can be used to reduce body temperature (Jansen, 1970). However, there was no evidence to suggest that the *H. nudus* specimens were using this method to slow their rate of heating. The relative humidities of 60%–70% used during the experiments, which mimicked conditions measured in the field, could have reduced the effectiveness of (but not eliminated) evaporative cooling (Edney, 1961). Although foaming behavior was not observed in the field, it is possible that it could reduce heating rates on warm days with low relative humidity (Thurman, 1998). Fiddler crabs (*Uca* species) are able to maintain a body temperature below that of the surrounding air by changing posture, blanching, and evaporating water from the body surface (Wilkins and Fingerman, 1965; Smith and Miller, 1973; Thurman, 1998). In the present study, there was no difference in heating or cooling rates when comparing live and dead animals (not shown), suggesting that there is no active mechanism that allows *H. nudus* to control the rate of heat gain or loss from the body.

When *H. nudus* was acclimated to different temperatures, an increase in the upper survival limits occurred as a result of the higher acclimation temperature; this has been reported previously for *H. nudus* (Todd and Dehnel, 1960), as well as for other species of crustaceans (Mundahl and Benton, 1990; Lagerspetz and Bowler, 1993; Korhonen and Lagerspetz, 1996; Cuculescu *et al.*, 1998; Stillman and Somero, 2000). However, much less is known about the critical thermal minima. In the present study, acclimation to a lower temperature extended the CTMin. Acclimation to a wider range of temperatures has also been shown to extend the CTMin range in other crustaceans (Layne *et al.*, 1987; Stillman and Somero, 1996).

Survival limits in air as a function of temperature have not been investigated previously for *H. nudus*. Interestingly, both the CTMax and CTMin were greater in air than in water. The heating and cooling rate in the incubator (0.5 °C/min) was adequate to allow equalization of the body with the surrounding air (unpubl. data; Fig. 2). These results are somewhat surprising: an animal would already be physiologically challenged by the switch in ventilatory media (Greenaway *et al.*, 1996), because an increase in air temperature decreases the oxygen-carrying capacity of the



hemocyanin and results in thermal acidosis (Morris *et al.*, 1996b). The CTMax was determined close to the body of the crab rather than by using internal temperature probes, which tended to tangle around the legs when the crabs were turned over, affecting the ability of the animal to right itself. Even though relative humidities in the incubator were high (60%–80%), a degree of evaporative cooling could have kept the body temperature a degree or so cooler than the surrounding air (unpubl. data; Fig. 2). This would suggest that the upper lethal limits in air were probably similar to those measured in water. However, if evaporative cooling reduced the body temperature, then the CTMin in air would also be expected to occur at a higher temperature than in water. This did not happen in the present study.

The thermal preference behavior of crabs acclimated to 10 °C and 16 °C, ascertained in a thermal gradient and by temperature-aversion experiments (Table 1), did not reflect their temperature tolerances: in both cases, 10 °C acclimated crabs had a higher temperature preference than those acclimated to 16 °C. In the temperature-aversion experiments, the oxygen tension was maintained at constant levels, so the emigration from water was a direct consequence of temperature. Indeed, aquatic hypoxia is not an impetus for emersion in this species (Morris *et al.*, 1996c). The air temperature that the crabs could exit into did not affect the exit temperature from the water (Table 1). This was unexpected, since acute exposure to higher air temperature (>15 °C) is costly and is associated with thermal acidosis and compensatory increases in cardiac output to maintain adequate oxygen uptake (Morris *et al.*, 1996a, b). Acclimation to 10 °C or 16 °C also influenced aversion behavior in air. When the air temperature was raised, crabs acclimated to 10 °C exited from under stones at a higher temperature than did 16 °C acclimated crabs. The adaptive significance of this behavior is unclear, since 16 °C acclimated crabs are more tolerant of higher temperatures (CTMax values). Thus, the effect of acclimation on behavior is apparently the opposite of its effect on survival regimes. In other reports on thermoregulatory behavior, lobsters that are acclimated to warm water choose warmer temperatures than do cold-acclimated individuals, possibly to maintain an optimal thermal regime for metabolic activities (Crossin *et al.*, 1998). When *Astacus astacus*, a crayfish, is acclimated to cold or warm water, this also directly affects thermal preference (Kivivuori, 1994). Acclimation to either 15 °C or 25 °C has no effect on the emersion response of the shore crab *Carcinus maenas*, which exits into air when the water temperature reaches 28 °C (Taylor and Wheatly, 1979). Likewise, acclimation to differing temperatures has no effect on the temperature preference of *Procambarus clarkii*, the red swamp crayfish (Espina *et al.*, 1993). In contrast to these responses, when the crayfish *Orconectes immunis* is acclimated to cold water, it tends to choose higher temperatures than animals

acclimated to warm water, yet no explanation is given for this paradox (Crawshaw, 1974).

Several factors can be eliminated as causes for the unexpected behavior observed in the present study. (1) The crabs were not responding to temperature increases of a particular magnitude, as occurs in lobsters (Cooke-Schreiber *et al.*, 2001). (2) The warming rate of the water (0.5 °C/min) was slow enough to allow the body temperature to equilibrate with the surrounding medium (Fig. 2). (3) Although the crabs were introduced into the apparatus in groups of five, this was unlikely to have a substantial effect on their behavior: they were roughly equal in size and there was ample shelter—both of these factors would reduce aggressive interactions between animals (Jacoby, 1981). (4) Although *Carcinus maenas* exhibits a behavioral hypothermia when exposed to hypoxic conditions (DeWachter *et al.*, 1997), this is probably not the case for *H. nudus* because oxygen levels were maintained during experiments and this species does not modify its behavior in response to hypoxia (Morris *et al.*, 1996c). (5) Finally, the acclimation period of 2 weeks should have been long enough for an increased temperature tolerance (Layne *et al.*, 1987; Cuculescu *et al.*, 1998). Indeed, rapid acclimation to thermal zones is an advantage for intertidal organisms: *H. nudus*, which acclimatizes within 48 h (Todd and Dehnel, 1960), is no exception.

When considering factors that could have influenced this overt behavior, it is worth noting that *H. nudus* could not be acclimated to temperatures greater than 16 °C without inducing widespread molting. Because the entire molting process can take several weeks (O'Halloran and O'Dor, 1988), it is possible that the 16 °C acclimated crabs were just starting to molt (D<sub>1</sub> or D<sub>2</sub> stage) without visible signs. Early stages of the molting process are associated with biochemical and physiological changes (see Chang, 1995) and make *H. nudus* less tolerant of high temperatures (Todd and Dehnel, 1960). The crabs acclimated to 10 °C would not undergo molting and could be expected to be more tolerant of the higher temperature regimes than the 16 °C acclimated crabs, which would avoid warmer temperatures. In addition, activity levels of cold-acclimated *Astacus astacus* decrease when these crayfish are warmed in water (Lehti-Koivunen and Kivivuori, 1994); if this were the case here for *H. nudus*, then cold-acclimated crabs would be less active and would not exhibit an escape response until a higher temperature.

Though all animals showed avoidance behavior when the temperature was increased, this was not the case when temperature was lowered. Only 30%–45% of the crabs emigrated from water and 20%–40% remained under shelters in the air. As expected, crabs acclimated to 10 °C appeared to emigrate at a lower temperature than those acclimated to 16 °C. However, since only animals that emigrated from the water or from under shelters were used in the analyses, this difference was not statistically signifi-

cant (Table 2). The reason that not all the animals exited when the temperature decreased becomes apparent when their long-term survival in extreme temperatures is considered. The crabs also did not recover after a few minutes of exposure at CTMax; they did, however, recover from cooling, even after several hours of exposure below CTMin. The same result is reported for *Astacus astacus* (Lehti-Koivunen and Kivivuori, 1994). Since *H. nudus* can survive exposure to low temperatures these crabs would not benefit from leaving the water or a protective shelter, where they would become vulnerable to predation.

The results of the shuttling experiments between air and water (Table 3) correspond to the behavioral patterns observed in the avoidance experiments. In cold water (10 °C), *H. nudus* individuals made fewer excursions into air; therefore the total time spent in air was also less (Table 3). At higher temperatures, the crabs were more active, making a greater number of excursions and spending a greater amount of time in air. In air, *H. nudus* is able to take up sufficient oxygen via an increased cardiac output (Morris *et al.*, 1996a, b). However, this is not without cost, especially at higher temperatures, where hemocyanin affinity and pH are affected to a greater degree, suggesting that oxygen delivery to the tissues declines when *H. nudus* breathes air at warm temperatures (Morris *et al.*, 1996a, b). Given these factors, the opposite behavior with respect to temperature may have been expected. However, as temperature increases in both air and water, so does oxygen uptake. The possible advantages of emigration from warm water into warm air could be a reduction in oxygen demand, as a consequence of evaporative cooling across the gills (Taylor and Wheatly, 1979). In addition, the CTMax values showed that the crabs tolerate higher temperatures in air than in water, which may explain why they spend more time in air at higher temperatures. In the present study, only two or three animals (tested at the 30 °C regime) spent longer than 5 h emersed (Table 3), whereas Greenaway *et al.* (1996) found that *H. nudus* can remain emersed for up to 8 h. These workers were using colder water temperatures (10–13 °C) than this animal is normally exposed to in summer (Gosselin and Chia, 1995). Thus, the crabs were probably moving into the warmer air (19–22 °C) due to a thermal preference rather than to the selection of a particular medium. To test this hypothesis, the behavior of *H. nudus* was investigated as crabs shuttled between air and water of differing temperatures, to determine if they were able to maintain the body temperature within a preferred range.

Although purple shore crabs are unlikely to encounter such extreme differences in air and water temperatures as shown in Figure 3, the results obtained suggest that they possess well-developed thermosensory mechanisms. The crabs tended to migrate to the air-water interface; although a slight microhabitat may have existed there, they exhibited a complex series of behaviors that suggested they were

using the thermal properties of both media to control body temperature (Fig. 3). The crabs raised or submerged their bodies in the shallow water of the chamber, thus gaining the benefits of evaporative cooling from the gills (Taylor and Wheatly, 1979) without the imbalances in pH and hemocyanin affinity caused by longer emersion in adverse temperature regimes (Morris *et al.*, 1996a, b, c). Maintenance of an optimal body temperature, rather than selection of a particular medium, appeared to be most important factor. In support of this conclusion, when water temperatures of 4–5 °C and air temperatures of 33–34 °C were offered (Fig. 3, trial 1), the crabs were able to maintain a body temperature of about 8–12 °C, independent of the two media (Fig. 4a). When air and water temperatures were reversed (Fig. 3, trial 7), the body temperature was still maintained within similar limits (Fig. 4b).

It was also important to investigate the thermoregulatory behavior of *H. nudus* in the field, since this species displays different behaviors in its natural environment (McGaw, 2001). Greenaway *et al.* (1996) suggest that *H. nudus* may routinely experience 10 °C differences in body temperature in the field. Certainly, the porcelain crab *Petrolisthes cinctipes*, which occupies a similar niche, may be exposed to temperatures under rocks in excess of 20 °C (Stillman and Somero, 1996). And even though *H. nudus* voluntarily exits into air in the laboratory (Greenaway *et al.*, 1996; Burnett and McMahon, 1987), this was not observed in any of the experimental animals in the field. They remained under rocks or deep in crevices during the intertidal period. This behavior has adaptive significance in that it keeps crabs in close contact with cover, thus avoiding the threat of predation (Low, 1970; Daly, 1981; McGaw, 2001). Indeed, *H. nudus* prefers to shelter underneath larger boulders, which provide the added advantages of heating or cooling more slowly (Stillman and Somero, 1996). Thus, using subtle movements within this thermal microhabitat, the crabs were able to maintain their body temperature independent of the surrounding air (Fig. 5). Additionally, the prevailing weather conditions can have a profound effect on the microhabitat and behavior of animals (Stillman and Somero, 1996). I have observed crabs active at low tide on humid or dull days; clearly other factors, in combination with temperature, play a role in emersion behavior and deserve further investigation.

*H. nudus* is well adapted for an existence in the intertidal zone (Morris *et al.*, 1996a, b, c; Greenaway *et al.*, 1996). The present study demonstrates that this species is able to detect differences in its thermal environment and use the thermal properties of both water and air to control its body temperature within a fairly narrow range. This study extends the work on thermoregulatory behavior in aquatic crustaceans (Crawshaw, 1974; Reynolds and Casterlin, 1979a, b, c, d; Lewis and Roer, 1988; Mundahl and Benton, 1990; Espina *et al.*, 1993; Kivivuori, 1994; Lehti-Koivunen and



Kivivuori, 1994; Crossin *et al.*, 1998) by examining the responses of an amphibious species during exposure to temperature change in both aquatic and aerial environments.

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